

*SILENE NELSONII*, A NEW LARGE-FLOWERED SPECIES FROM THE TRINITY RIVER  
AREA OF NORTHWESTERN CALIFORNIA, USA, AND A RE-EVALUATION OF  
*S. BOLANDERI* GRAY

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ABSTRACT

*Silene nelsonii* M.R. Mesler, M.S. Mayer, and S.K. Carothers (Caryophyllaceae), a species with large, day-blooming flowers from the Trinity River Basin of northwestern California, is described and illustrated. In the past, plants assignable to this new species have been referred to incorrectly as *S. bolanderi* A.Gray or *S. hookeri* Nutt. subsp. *bolanderi* (Gray) Abrams, names that rightfully apply to another member of the *Silene hookeri* complex. Here we argue that both *S. nelsonii* and *S. bolanderi* are worthy of recognition as separate species based on morphological distinction and a molecular phylogenetic analysis. *Silene nelsonii* differs from *S. bolanderi* by its more deeply lobed, white petals; lack of well-developed coronal petal appendages; densely ciliate petal bases; and shorter, sometimes branched sepal hairs. We present a key to the five members of the *S. hookeri* complex, all of which are in some degree rare in California and worthy of conservation concern.

Key Words: Caryophyllaceae, *Silene*, Trinity River, new species, rare.

Nuttall described *Silene hookeri* Nutt. in 1838 based on a type specimen collected near Portland, Oregon (Nuttall s.n., BM000582593!), and since then the name has been applied broadly to a group of low-growing perennials from western Oregon and northwestern California with large,  $\pm$  upright, day-blooming flowers with four-lobed petals (Hitchcock and Maguire 1947; Munz and Keck 1959; Peck 1961). Subsequent authors described five additional species for the group, based on differences in flower size, petal color, pattern of petal lobing, presence/absence of coronal petal appendages, degree of glandularity, and degree of stamen exertion. These species have been variously accepted, placed in synonymy, reduced to subspecies, or ignored in recent treatments (Table 1). For example, Asa Gray named *Silene bolanderi* (A.Gray) in 1868 based on specimens collected by Henry Bolander near Laytonville, in Mendocino County, California (*Bolander* 4696; holotype, GH00037857!). In his field notebook, Bolander described the plants as "... the finest species met with yet...[with] ...flowers of a very delicate pink color, large and showy." Gray regarded the species as "very...distinct" (Gray 1868), but later authors have disagreed about its status. Some included it as an un-named part of a broadly circumscribed *S. hookeri*, which also has pink flowers (Hooker 1873; Gray 1878; Watson 1880; Jepson 1925; Wilken 1993), while others treated it as a subspecies of *S. hookeri* (Abrams 1944; Hitchcock and Maguire 1947; Munz and Keck 1959; Smith and Wheeler 1990–1991; Morton, 2005). Recently, Hart-

man et al. (2012) resurrected the taxon as a distinct species in *The Jepson Manual*, 2nd ed. based on evidence presented by Nelson and Nelson (2004), a position adopted in the second volume of *Flora of Oregon* (Rabeler and Hartman, in press).

Our interest in the *S. hookeri* complex was motivated by examination of plants from Burnt Ranch, Trinity County, CA, whose white flowers have impressively long, narrow petal lobes and lack well-developed coronal petal appendages. These plants key to *S. bolanderi* in *The Jepson Manual*, 2nd ed., but our field and lab work has convinced us they do not match Gray's description of *S. bolanderi* or the type collection, which has pink petals and petal appendages. Here we describe the white-flowered plants as a new species, *S. nelsonii*, and present morphological and molecular phylogenetic evidence to show that it is worthy of recognition. We also argue that plants from Humboldt, Mendocino, Trinity, and Josephine counties that *do* match the original description of *S. bolanderi* represent a distinct species, separate from *S. hookeri*, and we present a key to the members of the *S. hookeri* complex.

TAXONOMIC TREATMENT

***Silene nelsonii*** M.R.Mesler, M.S.Mayer, & S.K.Carothers, sp. nov. (Figs. 1, 2, 5). – TYPE: USA, California, Trinity Co., 2.4 mi SW of Burnt Ranch, 0.75 mi from junction with FS 60 along FS 5N40, openings in mixed-age conifer forest, 25



TABLE 1. Varying opinions about the taxonomic treatment of the *Silene hookeri* complex. “+” = taxon recognized at the same level; “-” taxon neither recognized nor placed into formal synonymy; † = treatment published before taxon name.

|                                                            | Jepson<br>(1925) | Abrams<br>(1944)                           | Hitchcock and<br>Maguire (1947)               | Munz and<br>Keck (1959)                      | Peck<br>(1961) | Morton<br>(2005)                           | Hartman<br>et al. (2012) | Rabeler and<br>Hartman (2019)                   |
|------------------------------------------------------------|------------------|--------------------------------------------|-----------------------------------------------|----------------------------------------------|----------------|--------------------------------------------|--------------------------|-------------------------------------------------|
| <i>Silene hookeri</i> Nuttall ex.<br>Torrey & Gray (1838)  | +                | <i>S. hookeri</i> spp.<br><i>hookeri</i>   | <i>S. hookeri</i> spp.<br><i>hookeri</i>      | <i>Silene hookeri</i> spp.<br><i>hookeri</i> | +              | <i>S. hookeri</i> spp.<br><i>hookeri</i>   | +                        | <i>S. hookeri</i> spp.<br><i>hookeri</i>        |
| <i>S. bolanderi</i> Gray (1868)                            | -                | <i>S. hookeri</i> spp.<br><i>bolanderi</i> | <i>S. hookeri</i> spp.<br><i>bolanderi</i>    | <i>S. hookeri</i> spp.<br><i>bolanderi</i>   | -              | <i>S. hookeri</i> spp.<br><i>bolanderi</i> | +                        | +                                               |
| <i>S. ingramii</i> Tidestrom and<br>Dayton (1929)          | †                | -                                          | <i>S. hookeri</i> spp.<br><i>hookeri</i>      | restricted to OR                             | +              | -                                          | -                        | -                                               |
| <i>S. pulverulenta</i> Peck (1932)                         | †                | -                                          | <i>S. hookeri</i> spp.<br><i>pulverulenta</i> | restricted to OR                             | +              | -                                          | restricted to OR         | <i>S. hookeri</i> spp.<br><i>hookeri</i>        |
| <i>Silene serpenticicola</i> Nelson<br>& Nelson (2004)     | †                | †                                          | †                                             | †                                            | †              | +                                          | +                        | <i>S. hookeri</i> spp.<br><i>serpenticicola</i> |
| <i>Silene salmonacea</i> Nelson,<br>Nelson, & Erwin (2006) | †                | †                                          | †                                             | †                                            | †              | †                                          | +                        | restricted to CA                                |

May 2015, *M. R. Mesler 1642* (holotype: HSC; isotypes: UC, OSU, MICH).

*Diagnosis:* *Silene nelsonii* differs from *S. bolanderi* by its more deeply lobed white petals, lack of well-developed coronal petal appendages, relatively short, sometimes branched calyx hairs, and by its densely ciliate petal bases. *Silene nelsonii* differs from *S. hookeri* by its flaring, more deeply and more equally lobed petals, lack of well-developed coronal appendages, its radially symmetrical androecium, and densely ciliate petal bases.

*Description:* Perennial herbs; flowering shoots 2.5–25 cm tall, solitary or often in large clusters, arising at the tips of slender bracteate, rootless, branched or unbranched horizontal to ascending rhizomes that radiate from the crown of a deep taproot; above-ground stems simple to 1-branched, erect to decumbent, 0.6–22 cm long (not including pedicel of central flower), internodes 0.1–6.5 cm long, green to gray-green, sparsely pubescent to densely canescent, hairs simple, eglandular, straight or curled; lowermost leaves green, small, bract-like, +/- at ground-level, 2–17 mm long, 1.3–3.7 mm wide, 2–4 pairs of larger, larger cauline leaves above, green to gray-green, crowded to widely separated (in shade), petiolate or sessile, the largest subtending the inflorescence, 21.8–81.8 mm long, 5.8–18.9 mm wide, blade elliptic or oblanceolate to obovate, apex acute, base tapering to a +/- distinct petiole or not; inflorescence a 2–4 (7)-flowered cyme or flowers solitary, pedicels erect to ascending, canescent, eglandular, 0.5–7.5 cm long, deflexed in fruit, lowermost pair of bracts elliptic to narrowly oblanceolate, nearly as large as upper pair of cauline leaves, 13.9–61.0 mm long, 2.1–12.0 mm wide; flowers erect to ascending, 2.8–5.5 cm long, 2.5–6.8 cm wide, sometimes +/- as large as the above-ground vegetative body, diurnal, not fragrant, protandrous; calyx white-green or gray-green, 10-nerved, narrowly cylindric to clavate-obovoid, usually widest at or just above midpoint, narrowed at base of lobes, 11.8–23.5 mm long, 4.7–9.0 mm wide, expanded in fruit, base rounded or truncate, lobes narrowly triangular, acute to narrowly acute, sparsely to densely canescent, hairs simple or forked at base, eglandular, +/- opaque, straight or curled, sharp; anthophore pale green or white, glabrous, 1.3–5.0 mm long, 1.3–1.8 mm wide, length:width ratio 1.0–2.0; corolla narrowly to broadly funnel-shaped, white with a broad, translucent pale gray-green throat; petals initially ascending [early male stage], becoming recurved [late-male, female stage], not sharply bent at intersection of claw and limb, 20.2–50.0 mm; coronal appendages absent or present as inconspicuous white teeth, ≤1 mm long; claw longer than calyx, 12–23 mm, narrow at base, gradually expanded upward, translucent pale gray, with 2 +/- low white ribs, margin densely ciliate at base, hairs +/- obscuring gap between claw bases and antisepalous filaments; limb white, much wider than claw,



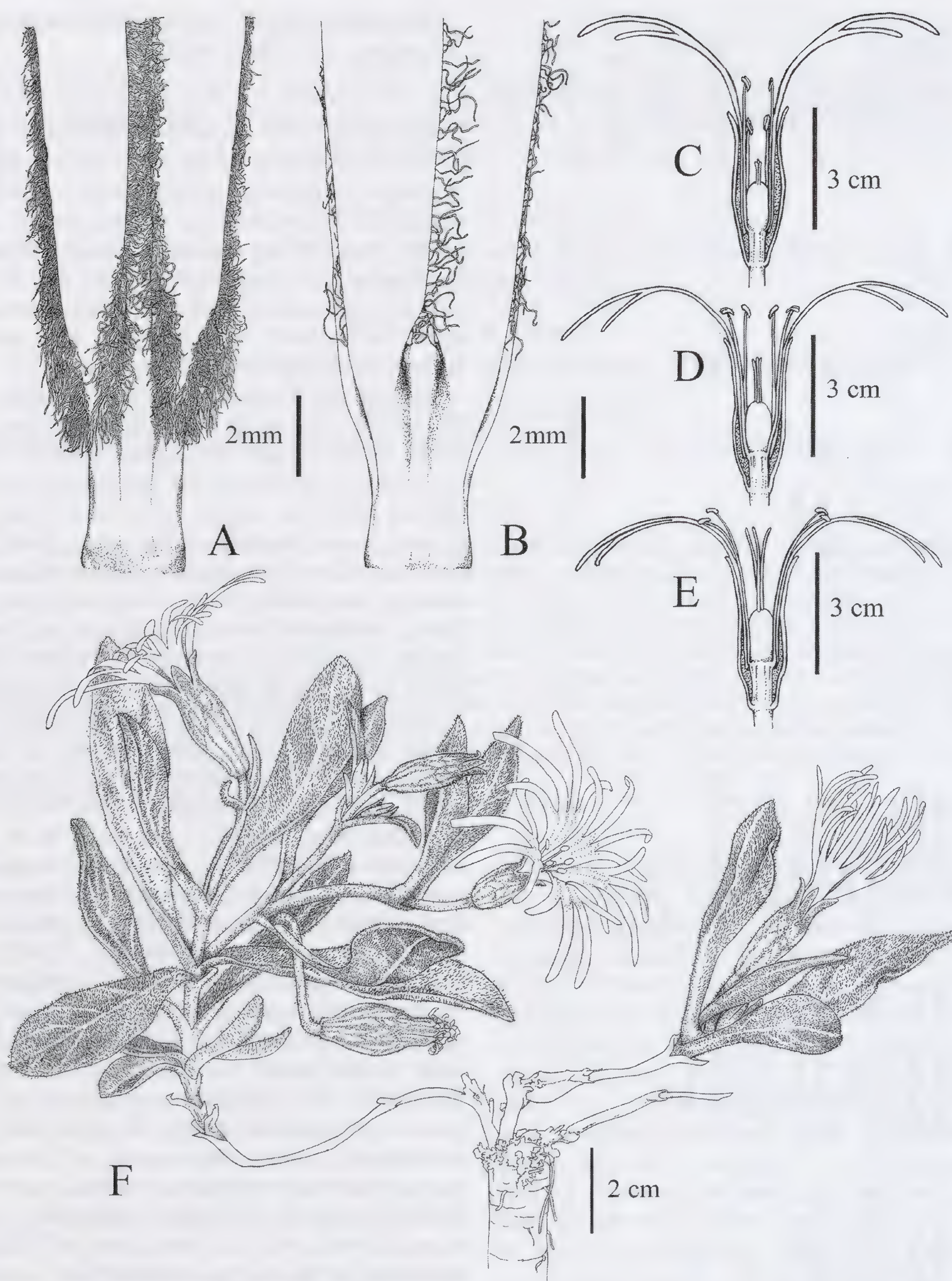


FIG. 1. Morphological features of *S. nelsonii* and *S. bolanderi*. *S. nelsonii* (A, C–F). *S. bolanderi* (B). A–B. Flower dissections showing anthophore, petal bases, and antisepalous filament base (partially obscured by hairs in A). C–E. Change in corolla shape in transition from male to female stages. F. Habit. Note post-anthesis flower with enlarged calyx at the tip of deflexed pedicel.

flabelliform, deeply 4-(6)-lobed, lobes of adjacent petals often overlapping; lobes usually extending to base of claw, narrow, linear to tapering from base or narrowly oblanceolate, 8.7–31.5 mm long, 1.0–3.0 mm wide (length:width ratio [3.5] 6–20.0), outer lobes  $\pm$  equal to inner lobes or shorter (inner:outer ratio 0.67–0.99), tips blunt to rounded to acute, sometimes notched; stamens in two sets of 5, shorter than or  $\pm$ -equal to claw, filaments radially arranged, white, initially erect as anthers dehisce, elongating and recurving onto petals [female phase], 12–22 mm;

anthers white, initially erect, becoming perpendicular to filament, members of each set dehiscing  $\pm$ -synchronously; styles 3, initially shorter than stamens and appressed [male phase], elongating and spreading with age, not strongly exerted when mature, curved at tip, 11–19 mm; ovary cylindrical to narrowly obpyriform, 4–5 mm long, 1.7–2.7 mm wide; capsule ovoid to globose, enclosed by persistent calyx, stalked,  $\pm$ -erect when maturing (via sharp bend at tip of pedicel), positioned at or near ground level at maturity, opening by 6 short,  $\pm$ -recurved



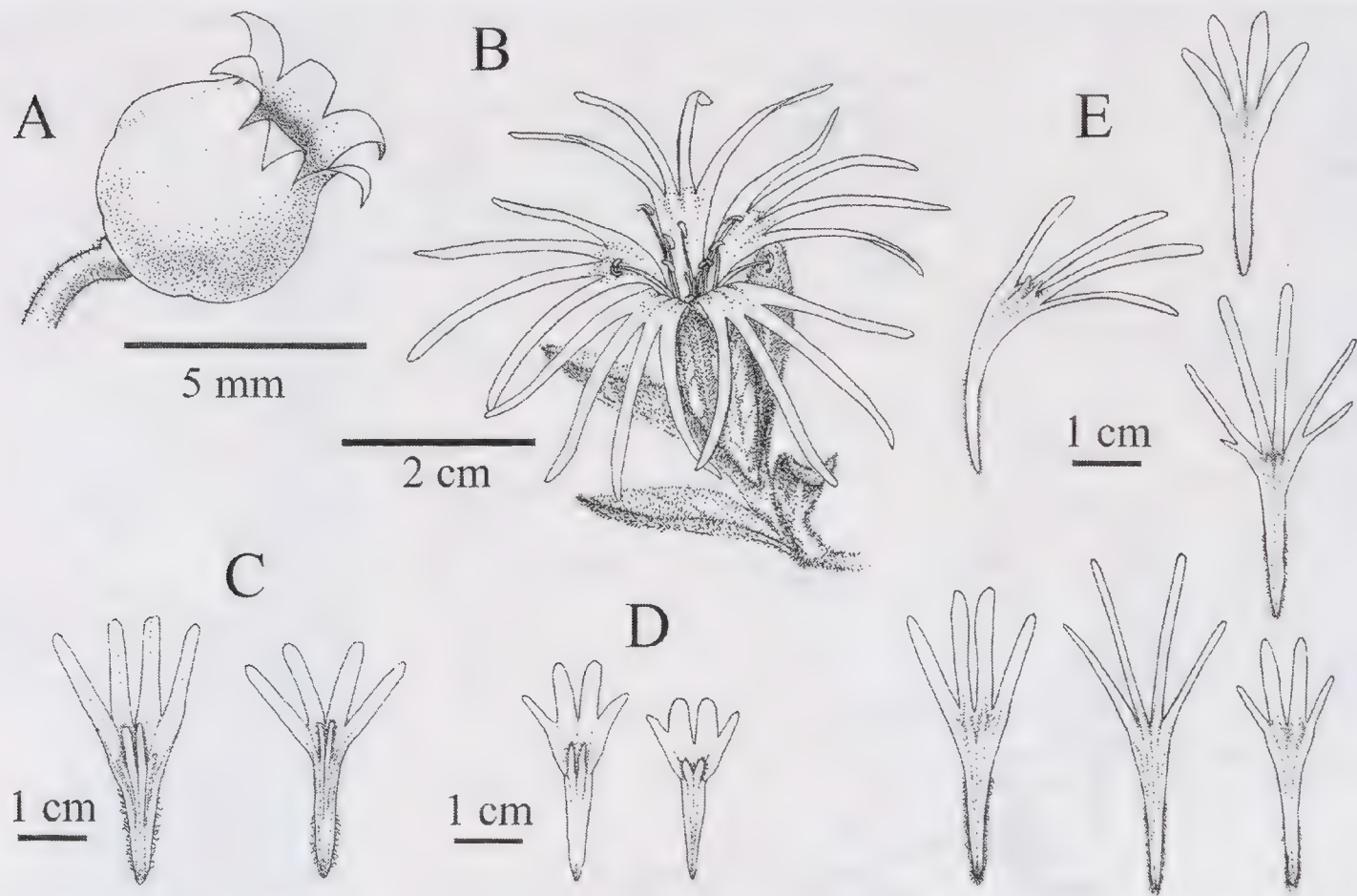


FIG. 2. Morphological features of *Silene nelsonii*, *S. bolanderi*, and *S. hookeri*. *S. nelsonii* (A, B, E). *S. bolanderi* (C). *S. hookeri* (D). A. Mature fruit. B. Male phase flower. C–E. Variation in petal lobing within and among species.

teeth, 6–10 mm long, 5.5–7.3 mm wide; seeds dark reddish brown, papillate, 2.0–2.25 mm long, 1.75–1.25 mm wide.

Paratypes (arranged alphabetically by collector within county. Note: locality information, including spatial coordinates (NAD 27), is provided only when given on the collection label. USA, California, **Humboldt County**: Brush Mountain, 26 May 1983, *Jimerson sn* (CAS); FS 5N40 about 3.2 miles from NF 60, 45°66'48"E, 45°12'644"N, 4092 ft, 3 Jun 2013, *Mesler 1481* (HSC); FS 6, 1 mile south of Sims Mtn, 44°91'17"E, 45°08'191"N, 3600 ft, 5 May 2018, *Mesler 1665a* (HSC); FS 6 near Manzanita Ranch, 45°39'45"E, 45°07'575"N, 1680 ft, 19 May 2018, *Mesler 1667* (HSC); Friday Ridge Road, near intersection with Hwy 299, 7 May 1978, *Reed 45* (HSC); Brannan Mountain, 7 July 1911, *Tracy 3414* (UC); **Trinity County**: Burnt Ranch USFS campground, 412 m, 30 April 1983, *Janeway 245* (HSC); Weaverville, *Kleeberger sn* (CAS); Hyampom Rd, west of Hayfork, 47°88'46"E, 44°91'662"N, 2100 ft, 7 June 2011, *Mesler* (HSC); Wildwood Rd, near Gemmill Gulch, 49°52'14 E 44°75'752 N, 3290 ft, 30 May 2010, *Mesler 818* (HSC); Weaverville, Garden Gulch Trail, 50°43'99 "E, 45°11'070"N, 2300 ft, 7 June 2010, *Mesler 821* (HSC); North of Hyampom along NF 60, 47°84'92"E, 44°91'919"N, 2300 ft, 29 May 2011, *Mesler 846* (HSC); south of Indian Valley Guard Station along NF 7, 47°53'73"E, 44°79'258"N, 4000 ft, 8 Jun 2011, *Mesler 852* (HSC); North of Indian Valley Guard Station on NF 10, 47°06'14"E, 44°87'503"N, 4050 ft, 8 Jun 2011, *Mesler 853* (HSC); Philpot Camp near Peanut, 48°39'61"E, 44°79'171"N, 2600 ft, 26 May 2013, *Mesler 1479* (HSC); FS 30°N01 near Wildwood, 50°00'28"E, 44°71'971"N, 4380 ft, 26 May 2013, *Mesler 1480* (HSC); Ewing Reservoir, Hayfork, 2440 ft, 48°58'17 E, 49°90'223"N, 2440 ft, 20 May 2018, *Mesler 1671* (HSC); south of Wildwood on FS

29N28, 49°41'19"E, 44°67'765"N, 27 Jun 2018, 4100 ft, *Mesler 1690* (HSC); FS 60 6.6 mi south of Hwy 299, 45°93'73"E, 45°13'111"N, 3500 ft, 30 May 1980, *Nelson 5347* (HSC67250); FS 60 10 mi south of Hwy 299, 4400 ft, 30 May 1980, *Nelson 5360* (HSC); 2 miles east of Burnt Ranch, 16 Jun 1964, *Spellenberg 438* (HSC); east side of Underwood Mtn Rd (5N09), ca. 4.9 miles south of Hwy 299, 12-June-1980, *Taylor 2855* (CHSC); near summit of Hayfork Mountain on Weaverville Rd 30 June 1923, *Tracy 6444* (UC); Burnt Ranch, 1500 ft, 27 April 1924, *Tracy 6655* (UC275265); north of Philpot campground, 2600 ft, 13 May 1979, *York 286* (HSC); **Shasta County**: Basin Gulch Camp, 50°33'55"E, 44°66'872"N, 2570 ft, 4 May 2013, *Mesler 1476* (HSC).

#### DISTRIBUTION AND HABITAT

*Silene nelsonii* is restricted almost entirely to Trinity County in an area bounded by the Main Stem and South Fork of the Trinity River. Exceptions are three sites due west of the Main Stem and another location between the South and Stuart Forks of the river (Figs. 3, 4). Plants generally grow in deep, well-drained soils in grassy openings near ephemeral drainages and along roads in cismontane woodland or lower montane coniferous forest at elevations of 85 to 1400 meters. Substrates are generally either ultramafic or metasediments. Common associates are *Ceanothus cuneatus* (Hook.) Nutt., *Festuca californica* Vasey, *Pinus jeffreyi* Grev. & Balf. in A. Murray, *P. ponderosa* Dougl. ex P. & C. Lawson, *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus garryana* Dougl. and *Q. kelloggii* Newb.

#### PHENOLOGY

*Silene nelsonii* flowers from mid-April to June; fruits begin to mature by late June.



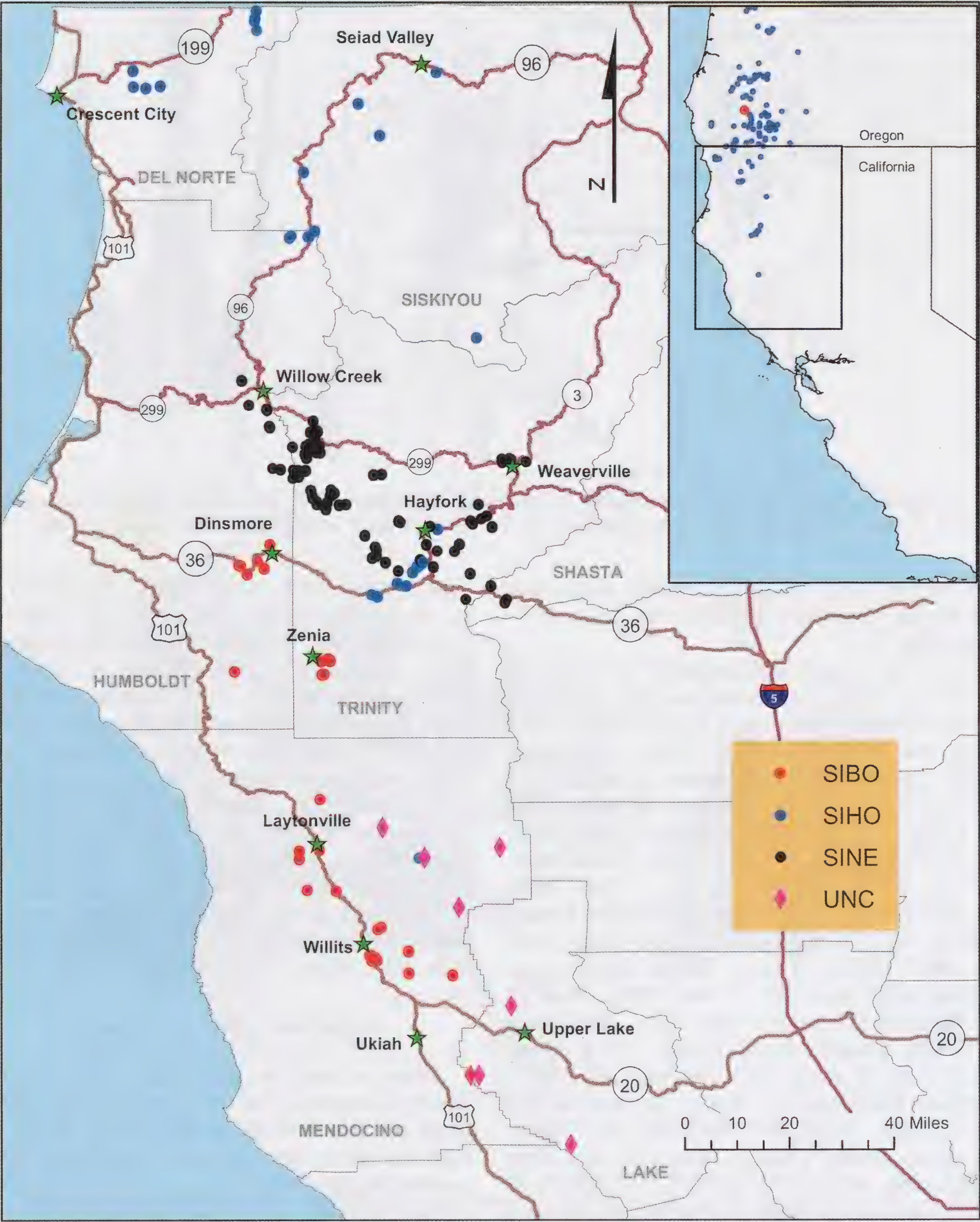


FIG. 3. Distribution of the *Silene bolanderi*, *S. hookeri*, and *S. nelsonii* in northwestern California. Inset shows full range of *S. hookeri* and the location of the Wolf Creek population in Josephine County, Oregon (red dot). SIBO = *S. bolanderi*; SIHO = *S. hookeri*; SINE = *S. nelsonii*; UNC = populations in Lake and Mendocino counties that could not be identified with certainty. Plotted occurrences based on herbarium records and recent observation.

ETYMOLOGY

The specific epithet *nelsonii* honors the late Thomas W. Nelson (1928–2006), who first drew our attention to the beautiful plants near Burnt Ranch. He was an avid student of the flora of northwestern California (Collections Manager, HSC, c. 1975–1985) and the first author of two species in the *Silene hookeri* complex (*S. salmonacea* T.W.Nelson,

J.P.Nelson & S.A.Erwin and *S. serpentinicola* T.W.Nelson & J.P.Nelson).  
Suggested common name: Nelson’s Stringflower.

MATERIALS AND METHODS

Description of the new species was based on examination of fresh material collected from most of the known occurrences, as well as specimens from the



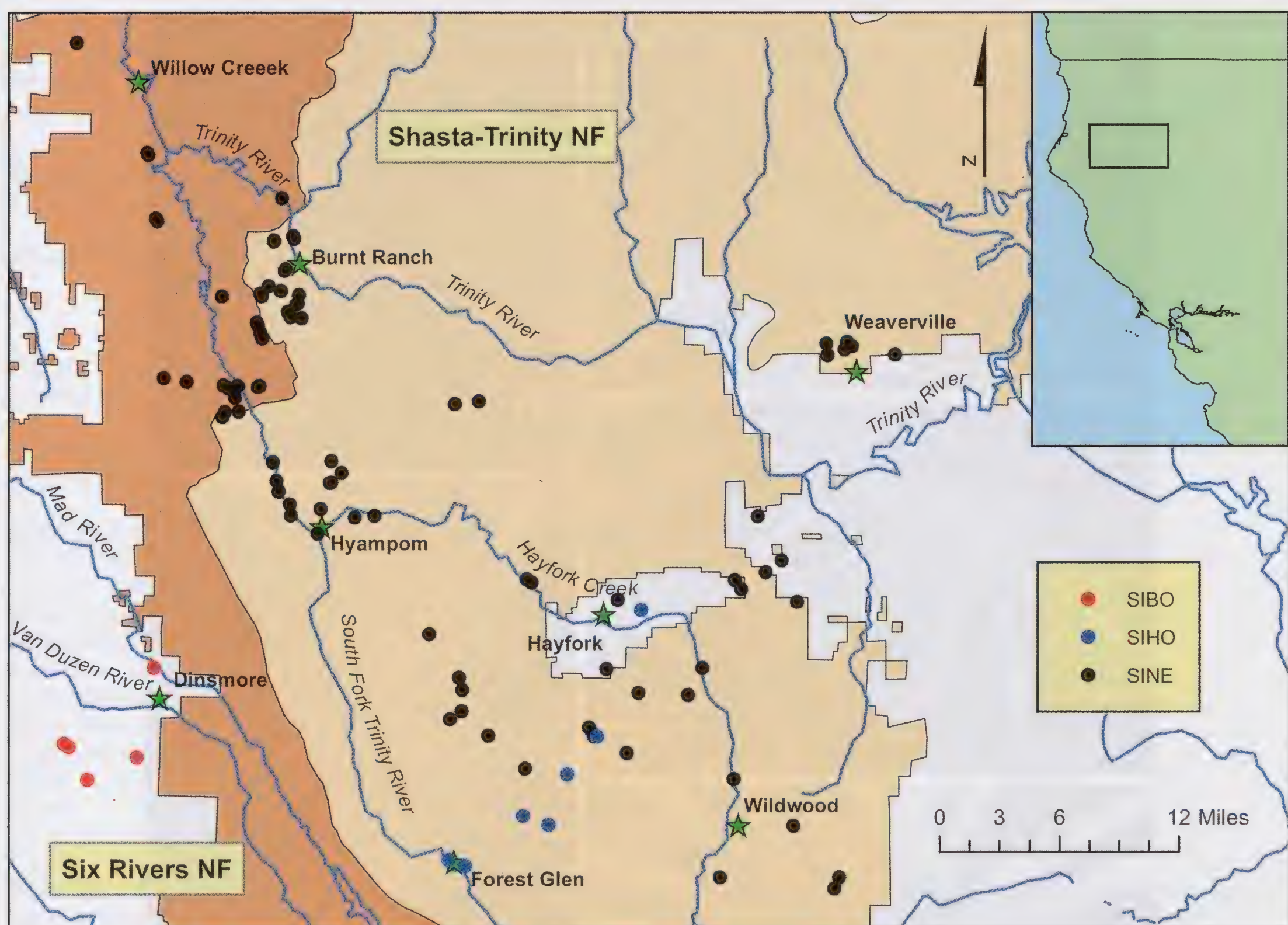


FIG. 4. Distribution of *S. nelsonii*. SIBO = *S. bolanderi*; SIHO = *S. hookeri*; SINE = *S. nelsonii*. All but two of the SINE occurrences confirmed extant by recent field work.

following herbaria: HSC, CAS, DS, JEPS, and UC. We also examined herbarium specimens, including online images of types (via JSTOR Global Plants), and fresh material from northwestern California and western Oregon representing the other elements of the *Silene hookeri* complex, here provisionally construed to include *S. bolanderi*, *S. hookeri*, *S. nelsonii*, *S. serpentinicola*, and *S. salmonacea* based on morphological similarity (Appendix 1). We treat *S. serpentinicola* as a distinct species (Nelson and Nelson 2004) – not as a subspecies of *S. hookeri* as proposed by Chambers and Meyers (2011) – based on newly discovered morphological differences between the two taxa (Mesler, unpublished data).

We could not locate the type locality of *S. bolanderi* (“Long Valley”), which presumably lies somewhere between Laytonville and Longvale (Mendocino County), but were able to study a few populations that match Gray’s concept of the species (and key to *S. hookeri* subsp. *bolanderi* in Hitchcock and Maguire 1947): Zenia Guard Station (Humboldt Co: Mesler 1195, HSC), Dyerville Loop (Humboldt Co: Mesler 1649, HSC); Tomki Road (Mendocino Co: Mesler 1187, HSC), and Wolf Creek (Josephine Co: Mesler 1183, HSC). The Wolf Creek population is one of approximately 20 reported from Josephine County in Oregon (S. Vrilakas, Oregon Biodiversity

Information Center, personal communication). Many historical occurrences of this taxon in California are apparently either extinct or located on inaccessible private property. Only two small populations of *S. hookeri* subsp. *pulverulenta* (M. Peck) C.L. Hitchc. & Maguire could be studied in the field (Jackson Co., Oregon: Mesler 1180, 1181, HSC), so description of *S. hookeri* is based on plants assignable to *S. hookeri* subsp. *hookeri* from Humboldt, Siskiyou, and Trinity counties in California, and Josephine and Douglas counties in Oregon per Hitchcock and Maguire (1947). Two confusing populations in Mendocino County that appeared intermediate between *S. bolanderi* and *S. hookeri* were also studied: Poonkinney Road (Wayman 283, HSC) and Rickabaugh Glade (Mesler 1185, HSC). For completeness, we include all five species in our key, but our morphological analysis focuses on comparisons of *S. bolanderi*, *S. hookeri*, and *S. nelsonii* because of the historical confusion about the boundaries of these taxa.

Examination of fresh flowers was critical because several important characters, such as the three-dimensional shape and diameter of the corolla, petal color, the presence/absence of coronal appendages, and the symmetry and pattern of maturation of the androecium, can be difficult or impossible to assess



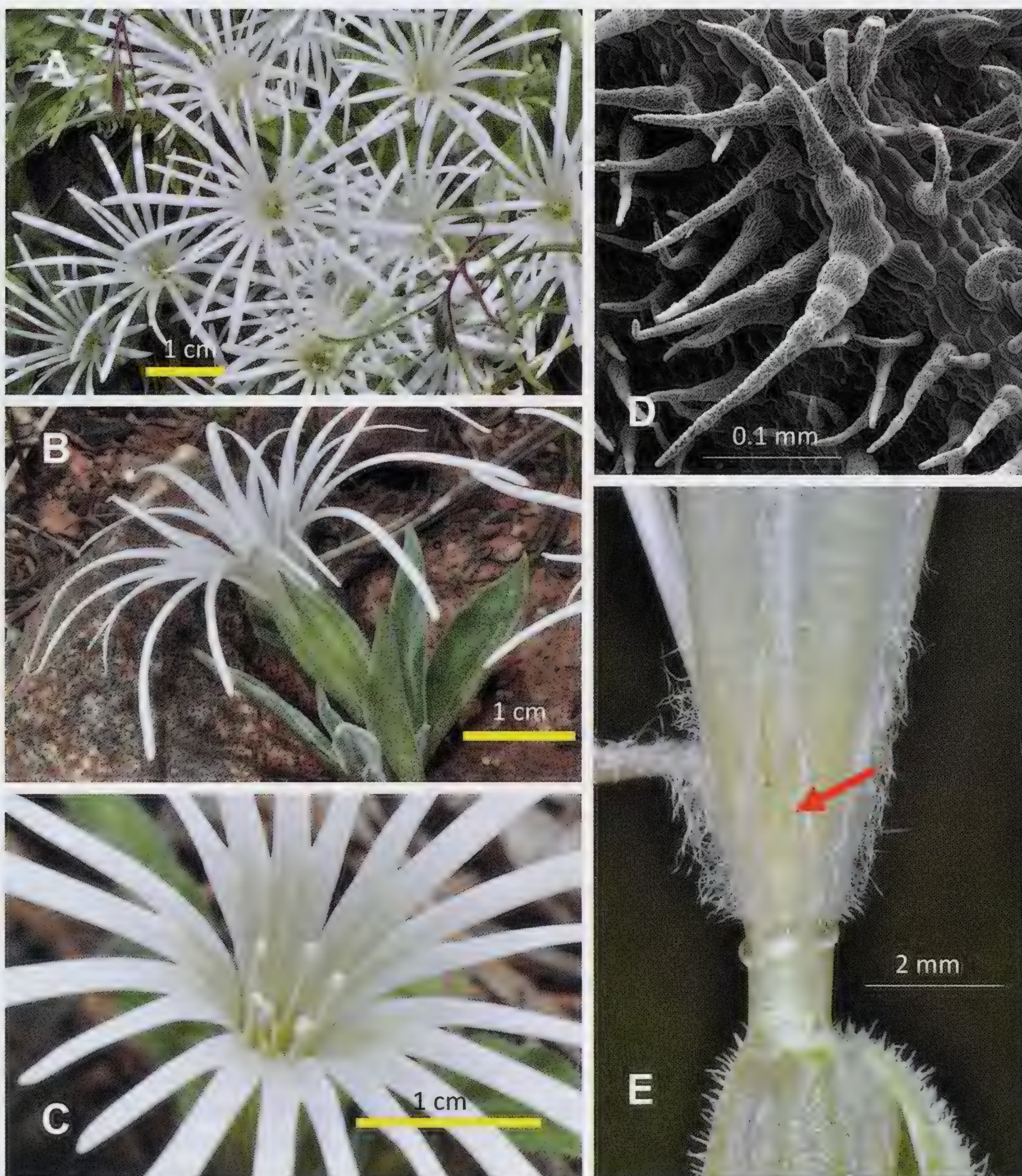


FIG. 5. *Silene nelsonii*. A. Philpot Campground, Trinity County, CA. B–D. Near Underwood Mountain, Humboldt County, CA. A. Individual petals difficult to discern because outer lobes of adjacent petals overlap. B. Flower larger than the vegetative body of the plant; note funnellform corolla. C. Inner antisepalous stamens with dehiscent anthers; note radial symmetry. D. Sepal hairs. E. Calyx dissected to show anthophore with nectar droplets; bases of two petals outlined by dense cilia. Nectar window and filament base (red arrow) obscured by petal hairs.

using dried material. Flower measurements were made using digital calipers, a dissecting microscope fitted with an ocular micrometer, or the computer program ImageJ (Rasband, 1997–2018). Petals were conveniently studied by flattening them on card stock, sprayed first with artist's adhesive, and then photographing with a ruler scale. The following measurements were taken for each petal: total length (measured from the base to the arc connecting the tips of the inner lobes); limb length (measured from the base of the coronal appendages); central sinus depth (measured from the sinus between the two inner lobes to the arc connecting the tips of the inner lobes); inner and outer lobe length (both measured from the level of one of the outer sinuses to the tip); inner and outer lobe width (both measured at the

level of one of the outer sinuses); and appendage length (measured as the part free from the petal surface). Additional traits were calculated as ratios based on these measurements (Table 2). Specimen sampling was not random, but instead focused on characterizing the range of trait values. Thus we do not report means, standard deviations, or statistical comparisons. Although generally reserved for sympetalous flowers, we use the terms salverform and funnellform because they aptly describe an important difference in overall corolla shape. We follow Jurgens (2006) in using the term anthophore (vs. carpophore) for the stalk-like structure that elevates the ovary above the calyx because it corresponds to the bases of the corolla, androecium, and gynoecium.



TABLE 2. FLORAL TRAITS USEFUL FOR DISTINGUISHING *SILENE BOLANDERI*, *S. HOOKERI*, AND *S. NELSONII*. Trait value ranges for the Poonkinney Road and Rickabaugh Glade populations are given, in that order, in brackets. See “Methods” for an explanation of petal measures.

|                                                            | <i>S. bolanderi</i>                                                                         | <i>S. hookeri</i>                                                                          | <i>S. nelsonii</i>                                                                   |
|------------------------------------------------------------|---------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|
| Corolla shape (male phase)                                 | narrowly to broadly<br>funnelform, petal limbs<br>ascending to recurved                     | salverform, petals limbs<br>+/- perpendicular to<br>claws                                  | narrowly to broadly<br>funnelform, petal limbs<br>ascending to recurved              |
| Corolla throat (male phase)                                | +/- broadly open; exposed<br>upper petal claws white<br>to pink, paired ridges<br>prominent | narrow; exposed upper<br>claws white to pink,<br>paired ridges prominent                   | broadly open; exposed<br>upper claws translucent<br>gray, paired ridges gen<br>weak  |
| Corolla diameter (mm)                                      | 27–58 [33–42; 24–43]                                                                        | 21–40                                                                                      | 16–75                                                                                |
| Corona appendages                                          | linear, >1 mm                                                                               | linear, >1 mm                                                                              | absent or inconspicuous<br>short teeth, gen <1 mm                                    |
| Petal length (mm)                                          | 29–42 [28–37; 25–30]                                                                        | 23–32                                                                                      | 20–56                                                                                |
| Petal limb color                                           | pale pink (rarely white)                                                                    | pale to deep pink (rarely<br>white)                                                        | white                                                                                |
| Petal limb length (mm)                                     | 14–23 [13–20; 12–17]                                                                        | 6–17                                                                                       | 9–33                                                                                 |
| Central sinus depth: limb<br>length ratio                  | 0.6–0.9 [0.5–0.7; 0.6–0.7]                                                                  | 0.3–0.9                                                                                    | 1                                                                                    |
| Inner lobe length (mm)                                     | 9–17 [4–10; 4–7]                                                                            | 2–10                                                                                       | 8–32                                                                                 |
| Outer lobe length (mm)                                     | 8–15 [4–10; 4 – 7]                                                                          | 1–7                                                                                        | 6–26                                                                                 |
| Inner lobe shape<br>(length:width ratio)                   | narrowly oblong to linear,<br>4–8 [2–4; 2–4]                                                | oblong, 1–5                                                                                | linear, 6–24                                                                         |
| Outer lobe shape<br>(length:width ratio)                   | 3 – 9 [2–6; 2–5]                                                                            | 1–6                                                                                        | 4–17                                                                                 |
| Outer vs. inner lobe length<br>ratio                       | 0.6–1.0 [0.5–0.9; 0.6–1.0]                                                                  | 0.4–1.0                                                                                    | 0.6–0.9                                                                              |
| Outer vs. inner lobe width<br>ratio                        | 0.6–1.1 [0.5–0.9; 0.6–1.0]                                                                  | 0.3–0.9                                                                                    | 0.7–1.6                                                                              |
| Petal base margin, visibility<br>of antisepalous filaments | glabrous, filaments clearly<br>visible                                                      | glabrous, filaments clearly<br>visible                                                     | sparsely to densely ciliate,<br>filaments at least<br>partially obscured by<br>hairs |
| Androecium symmetry,<br>within-whorl anther<br>dehiscence  | +/- radial, anther<br>dehiscence +/-<br>synchronous                                         | +/- bilateral, asynchronous                                                                | +/- radial, anther<br>dehiscence +/-<br>synchronous                                  |
| Calyx hairs                                                | simple, long, slender,<br>curled at tip, glandular<br>or not                                | simple or rarely branched<br>at base, long, slender,<br>curled at tip, glandular<br>or not | simple or branched at base,<br>relatively short, not<br>curled, not glandular        |

Twenty-seven populations were chosen to represent the geographic range and taxonomic diversity of the *S. hookeri* complex in the analysis of DNA sequence variation (Appendix 2). All but the Eden Valley population in Mendocino County (*Nelson 9118*) were studied in the field. *Silene laciniata* Cav. and *S. menziesii* Hook. serve as outgroups because they are, respectively, representatives of the tetraploid and diploid lineages that likely gave rise to allohexaploid *S. hookeri* (Popp and Oxelman 2007). However, because ITS vs. cpDNA topologies differ for *Silene* (Popp and Oxelman 2007), we used *S. laciniata* and *S. menziesii* to root the ITS tree, but just *S. laciniata* to root the cpDNA tree. One dried field-collected specimen per population provided tissue for total DNA extraction (Pepper and Norwood 2001) and PCR amplification. Four regions (*trnH* – *psbA*, *trnQ* – 5'*rps16*, *rpL16*, *rpS16*) in the chloroplast genome (cpDNA) were targeted because they have exhibited variation among closely related species across a wide sampling of spermatophyte taxa

(Shaw et al. 2005, 2007, including PCR primers and protocols). The internal transcribed spacer region (ITS-1, the 5.8s ribosomal RNA gene, and ITS-2) supplied an independent set of sequence data for a subset (21 of 32) of the specimens in the cpDNA data set. Primers (P17 and 26S-82R) and protocol for amplification of ITS followed Popp and Oxelman (2001, 2007), except that we lowered the annealing temperature to 54–56°C.

Sequencing of purified PCR products utilized the same primers as PCR, and was carried out by Retrogen, Inc. (San Diego, CA). Alignment of resulting sequences (See Appendix 2 for Genbank accession numbers) was done by eye; gaps were coded as missing data but indels were coded as additional binary characters following a simple indel coding strategy (Simmons and Ochoterena 2000). Highly variable microsatellite loci within these regions were excluded from the analysis. The four cpDNA regions were analyzed as a single data set, separate from the ITS data.



Phylogeny estimation employed Maximum Parsimony (PAUP\* version 4.0a build 162; Swofford, 2002) and Bayesian analyses (MrBayes v. 3.2.2; Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003). The parsimony analysis included 10 replicate heuristic searches with random addition of taxa, tree bisection-reconnection (TBR) branch-swapping, option DELTRAN, and equal-weighted characters. Bootstrap analysis of 1000 replicates using the “fast” option in PAUP\* was used to examine support for the clades. We used jModelTest 2.1.10 (Darriba et al. 2012) to identify the appropriate evolutionary models for the Bayesian analyses: HKY + I + G for the cpDNA segments, K80 for the ITS region. Analyses included one-million generations with four chains, sampling trees every 100 generations; a majority-rule consensus tree with posterior probabilities was constructed after a 25% burn-in.

## RESULTS

### Morphological Comparisons

*Silene bolanderi*, *S. hookeri*, and *S. nelsonii* resemble one another in several respects, both vegetatively and reproductively. In all three species, one to often several slender, shallowly buried rhizomes radiate from the crown of a deep tap root, and ultimately emerge as a cluster of simple or sparingly branched, decumbent to erect, aerial shoots (Fig. 1F). Each aerial shoot typically bears  $\leq 3$  closely spaced pairs of elliptical to narrowly oblanceolate leaves and one or a few showy flowers in a terminal dichasium. Stems and leaves are sparsely to densely canescent and green to gray-white. Except in relatively mesic sites, where internodes are longer, aerial shoots are often short ( $< 10$  cm) and flowers borne near ground level. Flowers of the three species are large (generally  $\geq 2.5$  cm across), upright or ascending, non-fragrant, day-blooming, and protandrous. Petals are differentiated into a narrow, +/- translucent claw and a greatly expanded, four-lobed limb. The margins of the claws overlap for most of their length forming a tube except at the very base, where five +/- elliptical gaps (“nectar windows”) provide access for pollinator proboscides to reach droplets of nectar that accumulate on the surface of the anthophore. The base of one of the five antisealous filaments bisects each gap (Figs. 1A, B, 5E, 6E). Two parallel ridges run up from about the distal one-third of the claw to the intersection with the limb. When present, coronal appendages emerge as extensions of these ridges. The androecium consists of two sets of five stamens, the antisealous maturing before the antipetalous. After pollination, pedicels elongate and bend sharply downward, bringing mature capsules to (or close to) ground level (Fig. 1F). Capsules are globose with an apical pore surrounded by six short recurved teeth (Fig. 2A).

*Silene bolanderi* and *S. nelsonii* share several floral features that set them apart from *S. hookeri* (Table 2). Both species have larger (diameter usually  $> 3.5$  cm), relatively open, deeply lobed flowers (ratio of central sinus depth:limb length at least 0.6). Petal lobes are usually long and slender (length:width ratio typically  $\geq 5$ ); inner lobes and outer lobes are approximately equal in size, although the outer lobes are usually at least slightly shorter and narrower at the base (Figs. 2B, C, E). As flowers of both species open and anthers begin to dehisce, the petal claws stand close together and +/- parallel inside the calyx, and petal limbs are oriented at approximately  $45^\circ$  to the claws (Fig. 1C), forming a narrow throat. But both claws and limbs diverge by the time styles begin to elongate, and petal lobes gradually arch and often recurve, resulting in a more open, narrowly to broadly funnelform corolla with a poorly defined broad throat, and exposing the upper surface of the claw (Figs. 1E, 2B, 5C, 6A, B, C). The androecium of both species is radially symmetrical, with stamens erect and +/- evenly spaced around the perimeter of the throat (Figs. 5C, 6C). Anthers in each set dehisce +/- synchronously. After dehiscence, filaments elongate and recurve onto the surface of the petals (Figs. 1E, 2B). In contrast, the flowers of *S. hookeri* are generally smaller (diameter usually  $\leq 3$  cm), and petals more shallowly and more unequally lobed (Table 2; Figs. 2D, 7A). Inner lobes are generally oblong, and outer lobes narrowly lanceolate or sometimes tooth-like (Figs. 2D, 7A). Like most other *Silene*, the petals of *S. hookeri* are bent at a +/-  $90^\circ$  angle at the intersection of limb and claw, forming a salverform corolla with a narrow, well-defined throat (Figs. 7A, B). Although stamens arise from the anthophore in radial fashion, some of the filaments tilt such that most or all of the anthers are positioned on one side of the corolla throat (Fig. 7B). Anthers within a set do not dehisce synchronously; typically, two of the five antisealous stamens open first, soon followed in sequential fashion by the remaining antisealous stamens and then by the antipetalous stamens.

The obvious differences between *S. hookeri* and *S. nelsonii* are consistent, but the distinction between *S. bolanderi* and *S. hookeri* appears to break down at two sites in Mendocino County (Table 2). The flowers of plants at Rickabaugh Glade fall into the range of *S. hookeri* in terms of petal color (dark pink), size, depth of petal lobing, and lobe shape, but overall corolla shape (relatively open with flaring petal limbs) and androecium symmetry are consistent with *S. bolanderi*. Flowers at the Poonkinney Road site are pale pink, relatively large and open, but petal limbs are more shallowly and unequally lobed than most *S. bolanderi*. Androecium symmetry at this site varies among individuals from +/- radial to bilateral. Based on examination of a limited number of difficult-to-interpret herbarium specimens, a few additional populations in eastern Mendocino and adjacent Lake counties (Fig. 3) may likewise prove





FIG. 6. *Silene bolanderi*. A. Zenia, Trinity County, CA. B. Tomki Road, Mendocino County, CA. C. Dyerville Loop Road, Humboldt County. A–C. Male phase flowers. Note radially arranged antisepalous stamens with dehiscent anthers and prominent coronal petal appendages in C. D. Sepals hairs. E. Calyx dissected to show anthophore; glabrous bases of two petals flank nectar window with clearly visible filament base (red arrow).

difficult to assign unambiguously to *S. bolanderi* or *S. hookeri* if eventually seen again in the field. This impression is supported by label annotations for two of these specimens, both identified as *S. hookeri* subsp. *bolanderi*. LeRoy Abrams annotated *Bacigalupi* 1526 (DS159849) as “intermediate between typical *hookeri* and subsp. *Bolanderi*,” and the collectors of *Hamann and Dearing* 1113A (JEPS) noted that “this ssp. is very variable as to its principle and purportedly diagnostic features.” The set of problematic specimens includes a collection from Eden Valley (*Nelson* 9118, HSC) that was included in the phylogenetic analysis.

*Silene nelsonii* can be distinguished from *S. bolanderi* most easily and reliably by differences in petal color, depth of petal lobing, expression of petal appendages, and vestiture at the base of petals (Table 2). The petal limb of *S. nelsonii* is consistently white; petal limb color in *S. bolanderi* is pale pink (Figs. 5,

6), although occasional white-flowered plants occur in some populations. Petals typically spread broadly in *S. nelsonii*, creating a broadly open flower center, which is pale translucent gray (sometimes with a faint green cast caused by reflections from the ovary and calyx, not pigmentation) (Fig. 5A, C). In contrast, the flower center of *S. bolanderi* is somewhat less open and white or pink (Fig. 6A–C). The petals of *S. nelsonii* are lobed to the base of the limb compared to generally less than 0.7 of the distance to the base in *S. bolanderi* (Figs. 2C, E, 6A–C). Like *S. hookeri*, the petals of *S. bolanderi* have well-developed coronal appendages at the intersection of claw and limb. These appear as extensions of the paired claw ridges, which are prominent and thick in this species (Figs. 2C, 6A–C). In contrast, the claw ridges of *S. nelsonii* are usually less robust, and most often end just proximal to the base of the inner petal lobes (Figs. 2E, 5C). In some cases, however, the ridges are more



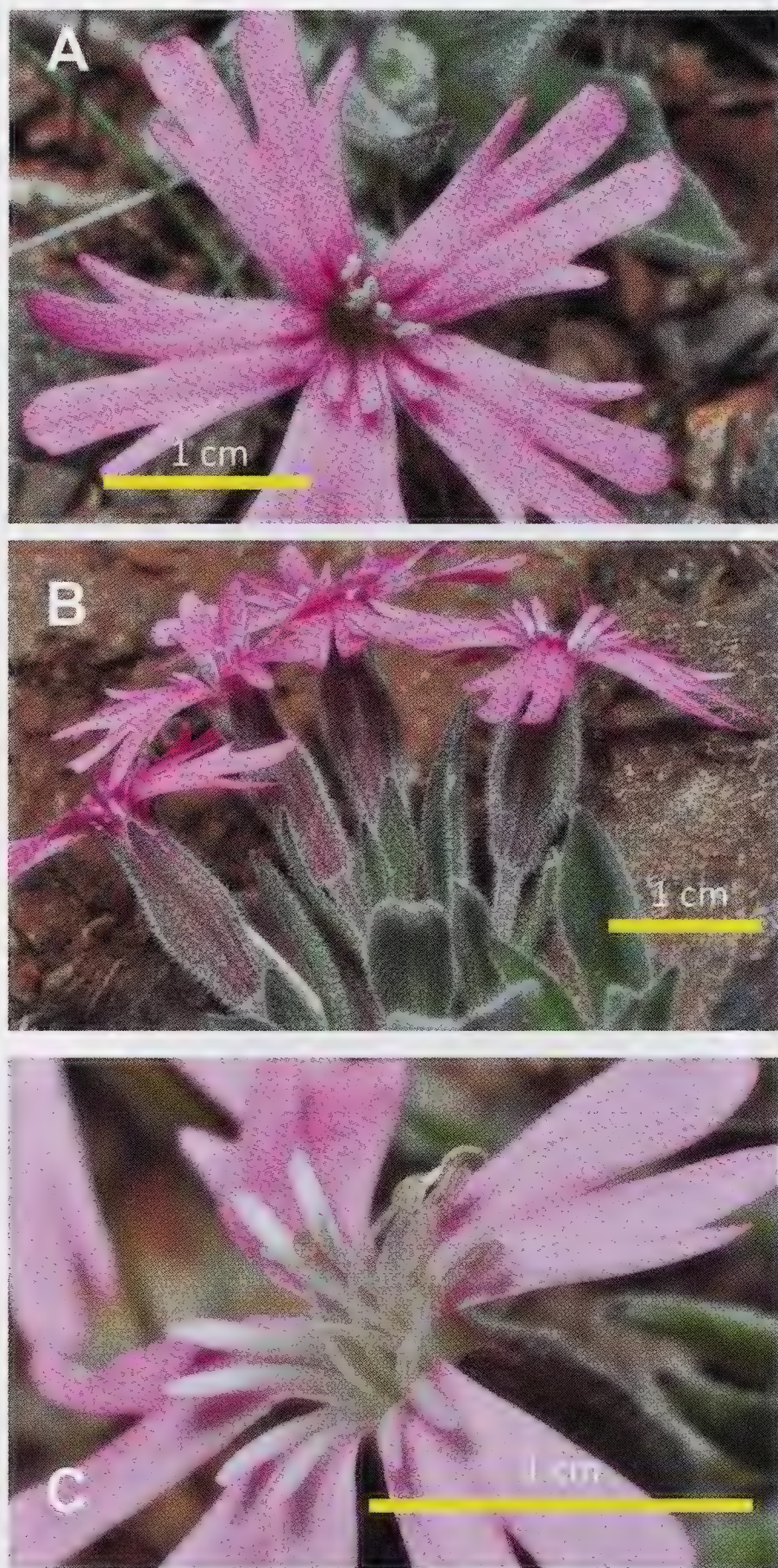


FIG. 7. *Silene hookeri*. A, B. French Hill Road. C. Philpot Campground, Trinity County. A. Petal limbs unequally and shallowly lobed; note position of anthers on one side of the throat. B. Bend at the juncture of limb and claw creates a salverform corolla. C. Female stage flower; note position of filaments on upper side of the throat.

robust and extend as short, rudimentary teeth. Petals of *S. nelsonii* are usually densely woolly ciliate at the base, and hairs cover the nectar window and underlying filaments (Figs. 1A, 5E). In contrast, the petal bases of *S. bolanderi* (and *S. hookeri*) are generally glabrous below the top of the nectar window and filament bases are clearly visible with a hand lens (Figs. 1B, 6E). Sepal hairs of *S. nelsonii* are non-glandular and typically relatively short and tapered from a broad base. In contrast, sepal vestiture in *S. bolanderi* varies from glandular to non-glandular within and among populations; non-glandular hairs are long, slender, curled at the tip, and unbranched (Figs. 5D, 6D). Flowers of *S. nelsonii* also tend to be larger with longer, narrower, and more strongly recurved petal lobes, but there is overlap for all of these traits (Table 2).

### Molecular Phylogenetic Analysis

The concatenated alignment of non-coding cpDNA sequences generated in the present study consisted of *trnH-psbA* (312 bases, 11 indels), *trnQ-5'rps16* (756 bases, 8 indels), *rpL16* (929 bases, 12 indels), and *rpS16* (891 bases, 12 indels). The ITS sequence alignment comprised 632 bases, with no indels. Strict consensus trees summarizing the results of the Maximum Parsimony and Bayesian analyses exhibited congruent topologies for the cp data, and likewise for the ITS data, thereby allowing reporting of the results using just two trees (Fig. 8). The clade of *Silene nelsonii* exemplars is recovered with 100% posterior probability and bootstrap confidence in both trees, sister to *S. menziesii* in the cp tree and to the clade of *S. bolanderi* + *S. hookeri* in the ITS tree. The contrasting position of *S. menziesii* in the two trees was unexpected, and was not influenced by outgroup choice. Morphologically unambiguous representatives of *S. bolanderi* form a strongly-supported clade in both trees with the exception of the plant sampled from Wolf Creek (Josephine County, Oregon), which shared no synapomorphies with the other *S. bolanderi* samples in the ITS tree. The morphologically ambiguous individual from Rickabaugh Glade nested as part of the *S. bolanderi* clade on both trees. In contrast, the representative from Poonkinney Road was nested within the *S. bolanderi* ITS clade, but sister to the entire *S. bolanderi* + *S. hookeri* clade in the cp tree. Finally, both cp and ITS topologies depict *S. hookeri* as non-monophyletic, regardless of the analytical approach.

### DISCUSSION

*Silene nelsonii* is arguably one of the most distinctive North American members of the genus. We base our decision to recognize it as a separate species on morphological differences, strong support from the molecular analysis, and almost complete geographical separation – evidence which, taken together, indicates an evolutionarily independent lineage. Earlier workers likely missed the obvious morphological distinction between *S. nelsonii* and *S. bolanderi* because they did not see *S. nelsonii* in the field owing to its restricted geographical distribution and because of the limited number of herbarium collections available for examination. A review of online databases and herbarium loans revealed only 15 collections assignable to *S. nelsonii* by 1947, when Hitchcock and Maguire published their revision of North American *Silene*. These authors examined two of the 15, both annotated as *S. hookeri* subsp. *bolanderi* (Abrams 7114, DS; Tracy 6655, UC). Only 65 collections were available by the time the *Flora North America* treatment of *Silene* was published (Morton 2005), 60% of which were held at HSC, hundreds of miles from major herbaria. Adding to the difficulty, even well-prepared pressed specimens of *S. nelsonii* and *S. bolanderi* can be difficult to



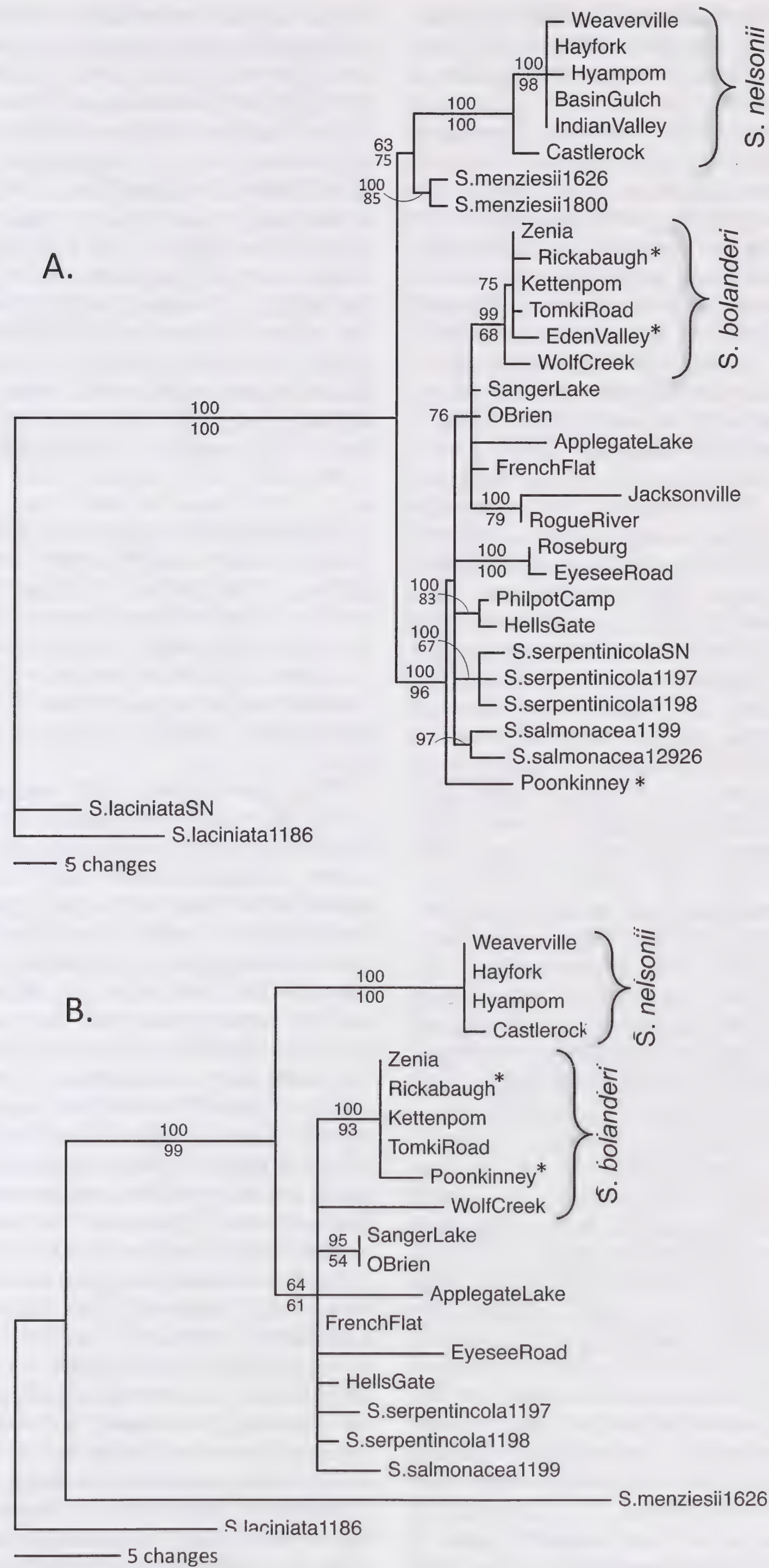


FIG. 8. Strict consensus tree of relationships among collections of *Silene* based on maximum parsimony analysis of (A) cpDNA sequence variation and (B) ITS region sequence variation. Location names outside of braces refer to *S. hookeri* collections; asterisks note morphologically ambiguous collections. Branch lengths are proportional to number of changes (substitutions and indels); if >50%, Bayesian posterior probability (upper) and bootstrap percentage (lower) accompany nodes. Three nodes on the cpDNA tree with low bootstrap support show Bayesian values only.



interpret. Critical differences that are readily apparent in the field (e.g., presence/absence of petal appendages, depth of petal lobing) are not always obvious in the herbarium.

We likewise believe that *S. bolanderi* should be treated as separate species, distinct from *S. hookeri*, but the application of the name *S. bolanderi* has a complicated history because previous authors who recognized the taxon (as a species or subspecies) appear to have confused it, at least partly, with *S. nelsonii*. For example, Hitchcock and Maguire's (1947) brief description of *S. hookeri* subsp. *bolanderi* is consistent with Gray's (1868) concept of *S. bolanderi*, but they cite two specimens of *S. nelsonii* as examples. The plants Nelson et al. (2006, Table 2) described as *S. bolanderi* and the ones that key to *S. hookeri* subsp. *bolanderi* in Morton (2005) are actually *S. nelsonii*. The description of *S. bolanderi* in Hartman et al. (2012) also matches *S. nelsonii*, with the exception of flower color and geographical range, which are given as white or pink and Outer North Coast Ranges (NCoRO), respectively. The flowers of *S. nelsonii* are never pink, and the species also occurs in the Klamath Region (KR). When properly circumscribed, *S. bolanderi* resembles *S. hookeri* in having pink petals with well-developed appendages, and in fact, the species has generally been treated as part of *S. hookeri* (Hooker 1873; Watson 1880; Gray 1878; Jepson 1925; Abrams 1944; Hitchcock and Maguire 1947; Munz and Keck 1959; Smith and Wheeler 1990–1991; Wilken 1993).

The case for recognizing *S. bolanderi* as a distinct species rests on a combination of morphological and molecular evidence. With only two exceptions, the differences between the *S. bolanderi* and *S. hookeri* populations we have seen in the field are obvious and striking, especially when two previously unappreciated traits – androecium symmetry and corolla form – are taken into account (Figs. 6, 7). In addition, all of the herbarium specimens of putative *S. bolanderi* we have examined from other sites in southern Humboldt and Trinity counties match the species based at least in flower size and petal lobe shape (other traits could not be scored reliably in all cases); the same is true for most historical collections from Mendocino County. Moreover, the California populations we sampled with unambiguous *S. bolanderi* morphology nest as part of a well-supported clade on both the cp and ITS trees. Placement of the Rickabaugh Glade population in this clade on both trees supports inclusion in *S. bolanderi* even though its flowers are smaller and less deeply lobed than other members of the species. In contrast, the apparent combination of *S. bolanderi*- and *S. hookeri*-like traits at Poonkinney Rd could indicate a history of hybridization between the two species, a hypothesis consistent with the incongruence of the cladogram topologies supported by cp and ITS sequences. The difficulty of interpreting herbarium specimens notwithstanding, a few other populations in eastern Mendocino and adjacent Lake counties

(Fig. 3) appear intermediate between the two species and together may comprise a narrow hybrid zone (see Appendix 1 and label comments on *Bacigalupi 1526* [DS] and *Hamann and Dearing 113A* [JEPS]). The two species may have hybridized in northwestern Oregon as well. The single plant we sampled from Wolf Creek (Josephine Co., Oregon) combined the chloroplast nucleotide sequence of *S. bolanderi* and the ITS sequence of the *S. hookeri* + *S. bolanderi* clade, although the plants in this population closely resemble *S. bolanderi* from California. Establishing the role of historical hybridization, if any, will require additional data, but current opportunities for hybridization between *S. bolanderi* and *S. hookeri* appear quite limited. At least in California, the two species are separated geographically (Fig. 3; most populations of *S. hookeri* occur north of *S. bolanderi*). We know of only one area where they apparently occur together (Eden Valley, Mendocino County; Smith and Wheeler, 1990–1991), but it is unclear if they are truly sympatric there because the locality is currently inaccessible (J. Wheeler, Bureau of Land Management, personal communication). In sum, although closely related to *S. hookeri*, available evidence supports recognition of *S. bolanderi* as an independent, morphologically distinguishable lineage.

Popp and Oxelman (2007) showed that *S. hookeri* is an allohexaploid derivative of hybridization between parental species belonging to the predominantly tetraploid clade (*Physolychnis s.l.*) that includes most North American *Silene* and a smaller, mainly diploid clade that includes *S. menziesii*. Based on their morphological similarity to *S. hookeri*, we propose that *S. bolanderi*, *S. nelsonii*, *S. salmonacea*, and *S. serpentinicola* were derived from the same allopolyploidization event and, along with *S. hookeri*, comprise a monophyletic complex of related species (named for the first species described in the group). This hypothesis receives support from our ITS cladogram, which resolves a strongly supported clade including all five species and separate from *S. laciniata* and *S. menziesii*. In contrast, the cp tree suggests that *S. nelsonii* should be excluded from the *S. hookeri* complex; it appears as sister to *S. menziesii* in a weakly supported clade that is sister to a group including *S. bolanderi*, *S. hookeri*, *S. salmonacea*, and *S. serpentinicola*. This result was unexpected given the strong morphological difference between *S. menziesii* and *S. nelsonii*, but it may signify that *S. nelsonii*, like some *S. menziesii*, is diploid and, in fact, that it was one of the parents of the *S. hookeri* complex. At present, chromosome numbers are known only for *S. hookeri* and *S. serpentinicola*, both of which are hexaploids (Kruckeberg 1960; Chambers and Meyers 2011). Numbers for the other species (especially *S. nelsonii*), as well as a more robust phylogenetic analysis with broader taxon sampling and additional nuclear genes, will be needed to determine the composition of the *S. hookeri* complex.



Plants assignable to *S. hookeri* on morphological grounds do not comprise a monophyletic group on either the cp or ITS tree (Fig. 8). One plausible explanation is that as the species spread to occupy its current range in northwestern California and southwestern Oregon, it gave rise to *S. bolanderi*, *S. salmonacea*, and *S. serpentinicola*, but otherwise remained little changed, and thus represents a plesiospecies (Olmstead 1995). Additional evidence will be needed to evaluate this proposal, but at this point we strongly favor retaining *S. hookeri*, *S. salmonacea*, and *S. serpentinicola* as separate species. An alternative approach, which combines all of them along with *S. bolanderi* into a single species, would unite morphologically distinctive elements that are almost certainly reproductively isolated from one another.

**Conservation implications.** Our study along with previous work by Thomas Nelson and colleagues (Nelson and Nelson 2004; Nelson et al. 2006) interprets *S. hookeri sensu lato* as a complex of five closely related species, all of which are in varying degrees rare in California and worthy of conservation concern. Both *S. salmonacea* and *S. serpentinicola* are currently listed as California Rare Plant Rank 1B.2 species based on their restricted distributions and limited number of occurrences (CNPS 2019). *Silene nelsonii* is likewise a narrow endemic, restricted to an area of about 1600 km<sup>2</sup> in central Trinity and adjacent Humboldt and Shasta counties in the vicinity of the Trinity River and its tributaries (Fig. 4). We know of more than 70 occurrences (separated by at least 0.4 km), which vary in size from fewer than 10 to well over 100 plants. Populations occur in relatively mesic grassy openings in mixed conifer-hardwood forests, along roads, or on exposed dry rocky slopes. The main microsite requirement appears to be relatively deep soils, which are required to allow development of long taproots. Potential threats include soil disruption or removal caused by road maintenance and expansion, trampling by grazing cattle, and severe fires that kill taproots. The species appears to benefit from canopy removal and moderate soil disturbance caused by logging, perhaps by creating bare soil for recruitment, but intense site preparation, herbicide use, and repeated disturbance resulting from industrial forestry practices are significant threats (J. K. Nelson, personal communication). Since many populations are large and apparently healthy and most occur on relatively remote public lands managed by the Shasta-Trinity National Forest, we recommend a California Rare Plant Rank of 4.3 (Plants Rare or Endangered in California and elsewhere; not very threatened in California, <20% of occurrences threatened) (CNPS 2019).

*Silene bolanderi* is more widely distributed than *S. nelsonii* but likely more sensitive. The species ranges from Mendocino to southern Humboldt and Trinity counties in California (Fig. 3) and occurs as a

cluster of disjunct populations in the northwestern corner of Josephine County, Oregon, where it is considered rare and “critically imperiled” (Oregon Biodiversity Information Center, 2019). Smith and Wheeler (1990–1991) regarded the species (referred to as *S. hookeri* subsp. *bolanderi*) as “locally common in northern Mendocino County” and J. P. Tracy noted on a specimen label (18880, UC1223229) that it was “frequent under oaks on Burr Valley Rd” (near Buck Mountain, Humboldt County), but our extensive field reconnaissance and conversations with expert regional botanists (G. Hulse-Stephens, C. Williams, T. Sholars) suggest that it may now be quite rare in California. Several historical collection sites occur on private lands that are no longer accessible, and a substantial area of potential suitable habitat remains unexplored across the range of the species. The number of extant California occurrences is uncertain, but likely quite small; we can confirm only 16. With the exception of newly discovered large populations near Zenia (Trinity County) and the large population at Rickabaugh Glade (Mendocino County), most of the known occurrences consist of 50 or fewer plants. Populations are vulnerable to ungulate grazing and trampling, road work, and conversion of habitat for high-value agriculture. We recommend a California Rare Plant Rank of 1B.2 (Plants Rare or Endangered in California and elsewhere; moderately threatened in California, 20–80% of occurrences threatened).

*Silene hookeri* is the most widely distributed species in the complex, with populations ranging from northwestern Mendocino County (single putative population at Eden Valley, *Wheeler* 349, BLMAR) through Humboldt, Trinity, Del Norte, and Siskiyou counties into western Oregon, where it is not considered rare (Fig. 3). In California, however, the species is known from only 18 scattered extant locations north of the Mendocino population, mainly in the Six Rivers, Siskiyou-Rogue, and Shasta-Trinity National Forests (Fig. 3). Additional exploration is warranted, but we recommend a rank of 2B.2 (Plants Rare or Endangered in California, but more common elsewhere, 20–80% of occurrences threatened) based on the limited number of occurrences and small size (<20 plants) of most of the populations.

**Identification.** The following key to members of the *S. hookeri* complex relies on floral traits and geography because we could not find vegetative or fruit differences that reliably separate the species. Identification of *S. salmonacea* and *S. serpentinicola* is straightforward based on obvious differences in petal color and geographical distribution (Nelson and Nelson 2004; Nelson et al. 2006). In contrast, identification of the other three species can be challenging because of substantial variation and overlap for generally useful traits like flower diameter, petal length, depth and equality of petal lobing, and expression of coronal petal appendages (Table



2). For example, *S. nelsonii* flowers are probably the largest among North American *Silene*, but flower diameter overlaps with *S. hookeri*, which has the smallest flowers in the complex. Overall corolla shape and androecium symmetry are more consistent, but are best evaluated before styles elongate because the petals spread apart and stamens change position as flowers age. Unfortunately, neither trait can be scored with certainty on herbarium specimens. The same is true for petal base vestiture, which is the single best way to recognize *S. nelsonii*. Some traits used in earlier treatments are problematic and not used here. For example, anther position, given as “included” for *S. hookeri* by some authors (Nelson and Nelson 2004; Nelson et al. 2006; Hartman et al. 2012), varies from slightly to distinctly exerted, and this character can be difficult to evaluate for taxa with broadly open corollas with poorly defined throats (*S. bolanderi*, *S. nelsonii*, *S. salmonacea*).

Hairs on the upper stems and calyces of *S. hookeri* subsp. *hookeri* are usually non-glandular (cf. Hartman et al. 2012, page 619; cf. Hitchcock and Maguire 1947, p. 44), but this trait varies within and among populations. The same is true for *S. bolanderi*. *Silene serpentinicola* is a strict serpentinophile; the other four taxa occur both on and off serpentine (cf. Hartman et al. 2012). With the exception of *S. hookeri*, species in the complex have more-or-less restricted, non-overlapping ranges, making geography useful for identification (Fig. 3). Evidently species in the complex are seldom sympatric; we have visited only two sites where pairs occur together (*S. nelsonii* and *S. hookeri* at Philpot Campground, Trinity Co.; *S. hookeri* and *S. serpentinicola* along French Hill Rd, Del Norte Co.). At both sites, we found a limited number of putative hybrid individuals with intermediate morphology and apparently aborted pollen.

KEY TO *SILENE HOOKERI* COMPLEX OF NORTHWESTERN CALIFORNIA AND WESTERN OREGON  
Our couplet 2 represents a proposed revision of the key by Hartman et al. (2012), starting at their couplet 38.

1. Petal limb red; calyx often reddish, hairs glandular; Del Norte Co., southern Curry Co. . . . . *S. serpentinicola*
- 1' Petal limb white, pink, or salmon-orange; calyx green or whitish green, hairs glandular or not
2. Petal limb salmon-orange or pink (rarely white); petal appendages conspicuous, consistent in size and shape; petal limb not lobed to base at center, inner lobes oblong to linear, <10 times longer than wide; petal bases glabrous or nearly so, antisepalous filaments clearly visible in nectar windows (elliptical gaps between petal bases) with hand lens; calyx hairs glandular or not
3. Petal limb salmon-orange, fading to pale red; center of flower (upper claw surface) bright to pale green; petal appendages short (<1 mm), tips sharp or blunt; calyx hairs not glandular; Trinity Co. north of Weaverville, within 8 km of Trinity Lake. . . . . *S. salmonacea*
- 3' Petal limb pale to bright pink (rarely white); center of flower pink or white; petal appendages linear, >1 mm, tips rounded to acute; calyx hairs glandular or not
4. Petal limb +/- perpendicular to claw as stamens dehisce, gen <15 mm, inner lobes gen oblong, gen <4× times longer than wide, apices rounded or blunt, outer lobes gen <6 mm; stamens gen clustered on one side of a narrow, well-defined throat (best evaluated after all 10 anthers have dehisced but before styles elongate); Humboldt, Mendocino [Eden Valley], Trinity, Siskiyou, Del Norte Cos., western Oregon. . . . . *S. hookeri*
- 4' Petal limb held at +/- 45 degrees in early male phase, spreading (sometimes recurving) as styles elongate, gen >15 mm, inner lobes narrowly oblong to linear, gen >5× longer than wide, apices rounded to acute, outer lobes gen >10 mm; stamens +/- evenly positioned around broader, less distinct throat; mainly south of Hwy 36 in California (Mendocino, southern Humboldt and Trinity Cos.), northwestern Josephine Co. in Oregon . . . . . *S. bolanderi*
- 2' Petal limb white; petal appendages absent or present as inconspicuous, weakly developed and variable short teeth; petal limb lobed to base, inner lobes linear, gen >10 times longer than wide; petal bases gen densely ciliate, antisepalous filaments gen obscured by hairs on petal margins; calyx hairs not glandular; Humboldt Co. (near Willow Creek), Shasta Co. (Harrison Gulch), Trinity Co. (mainly south of Hwy 299 and north of Hwy 36). . . . . *S. nelsonii*

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## APPENDIX 1

## ADDITIONAL SPECIMENS EXAMINED

*Silene bolanderi*

USA. CALIFORNIA. **Humboldt Co.:** *Anderson* 5698 (HSC); *Constance* 2612 (CAS, POM, RSA); *Eastwood* 4799 (CAS); *Kildale* 2204 (CAS); *Kildale* 10845 (CAS); *Mesler* 818 (HSC); *Mesler* 825 (HSC); *Mesler* 1633 (HSC); *Mesler* 1649 (HSC); *Montalvo* 493 (HSC); *Nelson* 444 (HSC);



*Nelson* 1849 (HSC); *Nelson* 5256 (HSC); *Parks* 791 (CAS, UC); *Tracy* 4234 (UC); *Tracy* 16283 (JEPS, UC); *Tracy* 18880 (UC); *Yates* 5719 (UC). **Mendocino Co.:** *Baker* 11502 a (UC); *Balls* 20756 (RSA); *Beane* 2020 (CAS, UC); *Bolander* 4696 (GH [G00037857], UC [8457], on-line images); *Davy* 5096 (UC); *Ferris* 11668 (CAS, UC); *Ferris* 11675 (CAS, RSA); *Head* s.n. (CAS); *Hutchison* 2432 (CAS, JEPS, RSA); *Jepson* 1853 (JEPS); *Kellogg* s.n. (CAS); *Kelly* s.n. (CAS); *Mason* 5273 (UC); *Mesler* 1187 (HSC); *Nelson* 815 (HSC); *Rattan* s.n. (CAS); *Smith* 6405 (CAS); *Smith* 6409 (CAS); *Wheeler* 975 (CAS); **Trinity Co.:** *Hoover* s.n. (HSC); *Kellogg* 86 (CAS); *Mesler* 817 (HSC); *Mesler* 854 (HSC); *Mesler* 855 (HSC); *Mesler* 1185 (HSC); *Mesler* 1194 (HSC); *Mesler* 1438 (HSC); *Nelson* 5336 (HSC); OREGON. **Josephine Co.:** *Mesler* 1183 (HSC).

### *Silene hookeri* ssp. *hookeri*

USA. CALIFORNIA. **Del Norte Co.:** *Baker* 816 (HSC); *Clifton* 3171 (HSC); *Jimerson* s.n. (HSC); *Kildale* 9950 (CAS); *Mesler* 856 (HSC); *Mesler* 1196 (HSC); *Mesler* 1201 (HSC); *Mesler* 1486 (HSC); *Muth* 4411 (HSC); *Overton* 4181 (HSC); *Renner* 2884 (HSC); *Tracy* 16197 (UC); *Tracy* 17192 (UC); *Tracy* 18910 (UC); *Van Deventer* s.n. (HSC); **Humboldt Co.:** *Chandler* 1539 (UC); *Kildale* 9137 (CAS); *Mesler* 1188 (HSC103745); *Mesler* 1482 (HSC); *Mesler* 1674 (HSC); *Smith* 9932 (HSC); *York* 168 (HSC); **Mendocino Co.:** *Wheeler* 349 (BLMAR); **Siskiyou Co.:** *Quick* 59-08 (CAS); *Rattan* s.n. (CAS); *Thomas* 4122 (CAS); *Tracy* 16273 (UC); **Trinity Co.:** *Chin* 60 (HSC); *Erwin* 100 (HSC); *Erwin* 101 (HSC); *Ferlatte* 2080 (HSC); *Ferris* 11690 (UC); *Howell* 30366 (CAS); *Jepson* 16648 (JEPS); *Mesler* 1189 (HSC); *Mesler* 1192 (HSC); *Mesler* 1652 (HSC); *Mesler* 1653 (HSC); *Mesler* 1654 (HSC); *Miller* 12 (HSC); *Sharsmith* 4372 (UC); *Sieburth* 10 (HSC). OREGON. **Benton Co.:** *Hansen* s.n. (CAS); *Johnston* (CAS); *Maw* s.n. (UC); *Nelson* 74 (CAS); **Douglas Co.:** *Abrams* 10504 (CAS); *Gale* 53 (CAS); *Gale* 192 (CAS); *Henderson* 12674 (UC); *Kimber* s.n. (CAS); *Mesler* 1184 (HSC); *Roantree* s.n. (CAS); *Thompson* 4393 (CAS); *Thompson* 4403 (CAS); *Thompson* 10156 (CAS); *Thompson* 10192 (CAS); *Wiley* s.n. (JEPS); **Jackson Co.:** *Applegate* 4220 (CAS); *Constance* 2939 (HSC); *Henderson* 5895 (CAS); *Mesler* 1179 (HSC); **Joesphine Co.:** *Abrams* 10356 (CAS); *Ackerman* 246 (HSC); *Applegate* 5040 (CAS); *Applegate* 7299 (CAS); *Breedlove* 3229 (CAS); *Dale* s.n. (CAS); *Eastwood* 1358 (CAS); *Gale* 7 (CAS); *Gale* 21 (CAS); *Gale* 208 (CAS); *Gale* 233 (CAS); *Goff* 108 (CAS, UC); *Gould* 798 (UC); *Gould* 1057 (UC); *Heller* 10039 (CAS); *Henderson* 95 (CAS, JEPS); *Hitchcock* 19104 (UC); *Howell* s.n. (CAS); *Jimerson* s.n. (HSC); *Kelly* 270 (HSC); *Kildale* 7911 (CAS); *Kildale* 9637 (CAS); *Mesler* 1178 (HSC); *Mesler* 1182 (HSC); *Weiler* 61191 (UC); *Olmstead* 98-24 (CAS); *Prescott* s.n. (CAS); *Renner* 2861 (HSC); *Ripley* 9594 (CAS); *Van Deventer* s.n. (HSC); **Lane Co.:** *Baker* 2769 (UC); *Constance* s.n. (CAS); *Peck* 22076 (CAS, UC); **Marion Co.:** *Gale* 214 (CAS); **Yamhill Co.:** *Gardiner* s.n. (Kew, K00728878).

### *Silene nelsonii*

USA. CALIFORNIA. **Humboldt Co.:** *Abrams* 7114 (CAS); *Baker* 2430 (HSC); *McRae* s.n. (HSC); *Newton* 117 (HSC); *Spjut* 1875 (HSC); *Tracy* 5999 (UC); **Shasta Co.:** *Alcasas* 91 (HSC); **Trinity Co.:** *Anderson* 2455 (HSC); *Baker* 2311 (HSC); *Baker* 2326 (HSC); *Barneby* 11551 (CAS); *Ferlatte* 2071 (HSC); *Ferris* 11688 (CAS, UC); *Goodyear* s.n. (CHSC); *Harris* s.n. (HSC); *Holman* s.n. (UC); *Junkans* s.n. (CAS); *Kildale* 10816 (CAS); *Linstedt* 25 (HSC); *Mesler* 844 (HSC); *Mesler* 847 (HSC); *Mesler* 849 (HSC); *Mesler* 851 (HSC); *Mesler* 1477 (HSC); *Mesler* 1484 (HSC); *Mesler* 1641 (HSC103776); *Mesler* 1668 (HSC); *Mesler* 1672 (HSC); *Mesler* 1673 (HSC); *Mesler* 1690 (HSC); *Montalvo* 257 (HSC); *Nelson* 4684 (HSC); *Nelson* 5175 (HSC); *Nelson* 5372 (CHSC); *Nelson* 5372 (HSC); *Nelson* 5394 (HSC); *Nelson* 5609 (HSC); *Nelson* 9121 (HSC); *Newton* 610 (HSC); *Oxner* 25 (HSC); *Sharsmith* 4359 (UC); *Smith* 8191 (HSC); *Specht* 191 (HSC); *Spellenberg* 167 (HSC); *Tate* 1416 (HSC); *Tate* 1445 (HSC); *Taylor* 1064 (CAS); *Taylor* 2917 (CHSC); *Wilson* s.n. (UC); *York* 3210 (HSC).

### *Silene salmonacea*

USA. CALIFORNIA. **Trinity Co.:** *Cantelow* 1246 (CAS); *Cantelow* s.n. (CAS); *Dayton* 369 (CAS); *Eastwood* 4947 (CAS); *Hoffman* 2446 (UC); *Janeway* 5024 (CHSC); *McClintock* s.n. (CAS); *Nelson* 9218 (HSC); *Smith* 12926 (HSC); *Taylor* 18097 (HSC); *True* 761 (UC); *Yates* 349 (UC).

### *Silene serpentinicola*

USA. CALIFORNIA. **Del Norte Co.:** *Baker* 1733 (HSC); *Barker* 643 (HSC); *Barker* 1611 (HSC); *Carothers* s.n. (HSC); *Clifton* 2560 (HSC); *Clifton* 3322 (HSC); *Clifton* 3365 (HSC); *Clifton* 5334 (HSC); *Clifton* 5397 (HSC); *Clifton* 7589 (HSC); *Deventer* s.n. (HSC); *Harris* s.n. (HSC); *Hoover* s.n. (HSC); *Imper* 1422 (HSC); *Imper* 1425 (HSC); *Imper* s.n. (HSC); *Jimerson* s.n. (CAS); *Jimerson* s.n. (HSC); *McRae* 208 (HSC); *Mesler* 1462 (HSC); *Mesler* 1463 (HSC); *Mesler* 1485 (HSC); *Mesler* 1486 (HSC); *Mesler* 1487 (HSC); *Nelson* 4151 (HSC); *Nelson* 4151 (HSC); *Nelson* 4164 (HSC); *Nelson* 4164 (HSC); *Nelson* 8736 (HSC); *Nelson* 8981 (HSC); *Nelson* 9085 (HSC); *Nelson* 9175 (HSC); *Renner* 582 (HSC); *Renner* 611 (HSC); *Renner* 626 (HSC); *Renner* 2844 (HSC); *Renner* 2848 (HSC); *Renner* 2850 (HSC6); *Renner* 2852 (HSC); *Renner* 2868 (HSC); *Renner* 2897 (HSC); *Renner* 2901 (HSC); *Renner* 2904 (HSC); *Renner* 2908 (HSC); *Renner* 2909 (HSC); *Renner* 2912 (HSC); *Renner* 2928 (HSC); *Renner* 2932 (HSC); *Smith* 6718 (HSC); *York* 906 (HSC).

### Species identification uncertain

USA. CALIFORNIA. **Lake Co.:** *Hamann* 1113A (JEPS); *Howe* 3091 (SDSU); *Lodge* 378 (UC); **Mendocino Co.:** *Bacigalupi* 1526 (CAS); *Eastwood* 15200 (CAS); *Janeway* 10474 (CHSC, on-line image); *Jones* 3814 (CAS); *Nelson* 9118 (HSC); *Smith* 2354 (CAS); *Smith* 6443 (CAS); *Wayman* 283 (HSC); *Wiggins* 12150 (CAS, UC).



APPENDIX 2  
GENBANK ACCESSION NUMBERS  
SIBO = *S. bolanderi*; SIHO = *S. hookeri* ssp. *hookeri*; SIHOPU = *S. hookeri* ssp. *pulverulenta*; SILA = *S. laciniata*; SINE = *S. nelsonii*; SISA = *S. salmonacea*; SISE = *S. serpentinicola*; UNC = species identification uncertain. All vouchers held at HSC.

| Locality       | Taxon  | State: county | Collection       | trnH     | trnQ     | rpL16    | rpS16    | ITS      |
|----------------|--------|---------------|------------------|----------|----------|----------|----------|----------|
| Kettenpom      | SIBO   | CA: Trinity   | Mesler (855)     | MN231096 | MN231128 | MN231159 | MN231191 | MN231221 |
| Rickabaugh     | SIBO   | CA: Mendocino | Mesler (1185)    | MN231095 | MN231127 | MN231158 | MN231190 | MN231220 |
| Tomki Road     | SIBO   | CA: Mendocino | Mesler (1187)    | MN231098 | MN231130 | MN231161 | MN231193 | MN231223 |
| Wolf Creek     | SIBO   | OR: Josephine | Mesler (1183B)   | MN231097 | MN231129 | MN231160 | MN231192 | MN231222 |
| Zenia          | SIBO   | CA: Trinity   | Mesler (854)     | MN231094 | MN231126 | MN231157 | MN231189 | MN231219 |
| Applegate Lake | SIHO   | OR: Jackson   | Mesler (1179)    | MN231102 | MN231134 | MN231165 | MN231197 | MN231227 |
| Orleans        | SIHO   | CA: Humboldt  | Mesler (1188)    | MN231105 | MN231137 | MN231168 | MN231200 | MN231229 |
| French Flat    | SIHO   | OR: Josephine | Mesler (1182)    | MN231103 | MN231135 | MN231166 | MN231198 | MN231228 |
| Roseburg       | SIHO   | OR: Douglas   | Mesler (1183A)   | MN231104 | MN231136 | MN231167 | MN231199 | —        |
| Hell's Gate    | SIHO   | CA: Trinity   | Mesler (1192)    | MN231107 | MN231139 | MN231170 | MN231202 | MN231230 |
| O'Brien        | SIHO   | OR: Josephine | Mesler (1178)    | MN231101 | MN231133 | MN231164 | MN231196 | MN231226 |
| Philpot Camp   | SIHO   | CA: Trinity   | Mesler (1189)    | MN231106 | MN231138 | MN231169 | MN231201 | —        |
| Sanger Lake    | SIHO   | CA: Del Norte | Mesler (856)     | MN231100 | MN231132 | MN231163 | MN231195 | MN231225 |
| Jacksonville   | SIHOPU | OR: Jackson   | Mesler (1180)    | MN231109 | MN231141 | MN231172 | MN231204 | —        |
| Rogue River    | SIHOPU | OR: Jackson   | Mesler (1181)    | MN231110 | MN231142 | MN231173 | MN231205 | —        |
| Cow Mtn        | SILA   | CA: Mendocino | Mesler (1186)    | MN231119 | —        | MN231182 | MN231214 | MN231235 |
| Weitchpec      | SILA   | CA: Humboldt  | MacIntosh (s.n.) | MN231118 | MN231150 | MN231181 | MN231213 | —        |
| Silver Lake    | SIME   | CA: Lassen    | Mesler (1626)    | MN231116 | MN231148 | MN231179 | MN231211 | MN231234 |
| Deer Creek     | SIME   | CO: Jefferson | Wittmann (1800)  | MN231117 | MN231149 | MN231180 | MN231212 | —        |
| Basin Gulch    | SINE   | CA: Shasta    | Mesler (1476)    | MN231091 | MN231123 | MN231154 | MN231186 | —        |
| Castlerock     | SINE   | CA: Trinity   | Mesler (1481)    | MN231092 | MN231124 | MN231155 | MN231187 | MN231218 |
| Hayfork        | SINE   | CA: Trinity   | Mesler (844)     | MN231089 | MN231121 | MN231152 | MN231184 | MN231216 |
| Hyampom        | SINE   | CA: Trinity   | Mesler (849)     | MN231090 | MN231122 | MN231153 | MN231185 | MN231217 |
| Indian Valley  | SINE   | CA: Trinity   | Mesler(1484)     | MN231093 | MN231125 | MN231156 | MN231188 | —        |
| Weaverville    | SINE   | CA: Trinity   | Mesler (821)     | MN231088 | MN231120 | MN231151 | MN231183 | MN231215 |
| Trinity Center | SISA   | CA: Trinity   | Smith (12926)    | MN231115 | MN231147 | MN231178 | MN231210 | —        |
| Trinity Dam    | SISA   | CA: Trinity   | Mesler (1199)    | MN231114 | MN231146 | MN231177 | MN231209 | MN231233 |
| Humboldt Flat  | SISE   | CA: Del Norte | Mesler(1197)     | MN231112 | MN231144 | MN231175 | MN231207 | MN231231 |
| Gasquet Mtn    | SISE   | CA: Del Norte | Mesler (1198)    | MN231113 | MN231145 | MN231176 | MN231208 | MN231232 |
| French Hill    | SISE   | CA: Del Norte | Mesler (sn)      | MN231111 | MN231143 | MN231174 | MN231206 | —        |
| Eden Valley    | UNC    | CA: Mendocino | Nelson (9118)    | MN231108 | MN231140 | MN231171 | MN231203 | —        |
| Poonkinney     | UNC    | CA: Mendocino | Wayman (283)     | MN231099 | MN231131 | MN231162 | MN231194 | MN231224 |